

A PRELIMINARY STUDY OF THE PLANKTON OF THE CLEVELAND HARBOR AREA, OHIO. III. THE ZOOPLANKTON, AND GENERAL ECOLOGICAL CONSIDERATIONS OF PHYTOPLANKTON AND ZOOPLANKTON PRODUCTION¹

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During the year September, 1950 through September, 1951, a study was made of the Cleveland Harbor area in connection with a survey of pollution conditions in Lake Erie. The chemical and physical results of this study were previously reported by Davis (1953) and Davis and Roney (1953). The results of the phytoplankton analyses were reported by Davis (1954). It is the purpose of the following paper to describe the results of the analysis of the zooplankton obtained in the plankton samples, and in addition to discuss the dynamic interrelations of the plankton and the environment. The relationship of the plankton to pollution is being discussed elsewhere.

Collections and procedures

Twenty-three trips were undertaken between September 15, 1950 and September 30, 1951. Weather conditions permitting, nine stations were occupied as follows (fig. 1):

- Station 1. Under the railroad bridge near the mouth of the Cuyahoga River.
- Station 2. Between W Pierhead Light and E Pierhead Light at the mouth of the jetties.
- Station 3. Halfway between the jetties and Cleveland Division of Water and Heat Intake Crib No. 3.
- Station 4. At Intake Crib No. 3.
- Station 5. Near red bouy No. 2, off the foot of E 17th St., inside the breakwater.
- Station 6. Off the foot of E 40th St., inside the breakwater.
- Station 7. Off E Entrance Light, inside the breakwater.
- Station 8. Outside the breakwater, opposite station 6.
- Station 9. Outside the breakwater, opposite station 5.

At each station, both at the surface and at a depth of 6.5 m. (which was about one meter above the bottom at all stations except the deeper stations 3 and 4), two plankton samples were obtained. At each level one of these samples consisted of approximately 250 ml. of unfiltered water, preserved with 15 ml. of 40 percent formaldehyde, subsequently centrifuged. The second sample was obtained by the use of a Juday plankton trap of 10 liter capacity. This also was preserved with formalin. In addition to the quantitative samples, two qualitative samples were obtained in the cleanest water visited on each trip (usually in the vicinity of stations 4 or 7) by the use of small cone nets made of No. 20 and No. 12 mesh silk bolting cloth. Chemical and physical observations also were made at each station, as described by Davis and Roney (1953) and Davis (1953).

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Experience showed that the samples obtained by the use of the Juday plankton trap were more satisfactory, especially for the analysis of the zooplankton. Therefore, except where mechanical failure of the trap, or other misfortune prevented the collection of satisfactory trap samples, the centrifuged samples were not analysed. The report below, except where indicated, is based upon the analysis of the trap samples only.

Trap samples were analysed, in most cases, as follows: the preserved sample was adjusted to a convenient known volume, and a 1 ml. aliquot was placed in a Sedgwick-Rafter plankton counting cell. Common organisms encountered in a given number of the fields delimited by a Whipple ocular micrometer were counted, using the low power (100 X) of a compound microscope. The number of counted fields varied with the abundance of the organisms, and ranged from an occasional

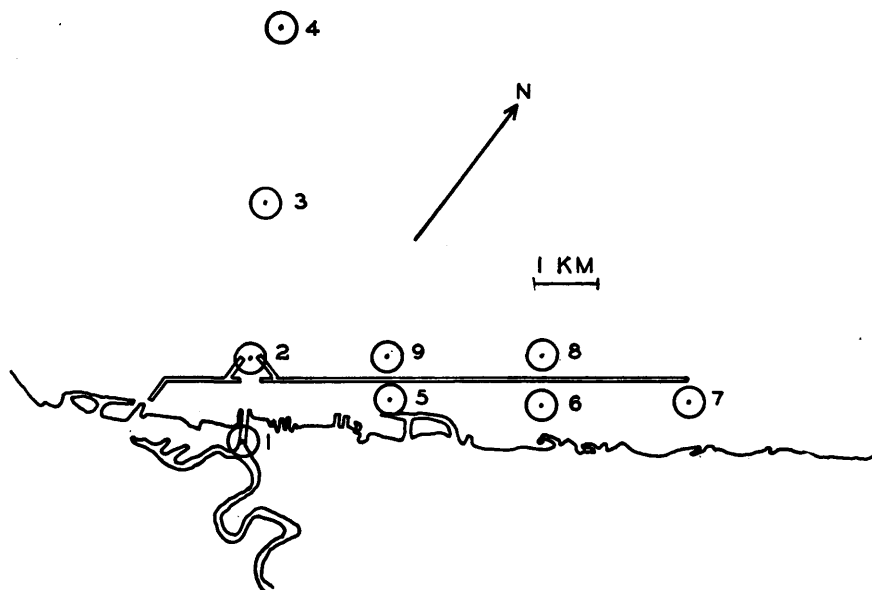


FIGURE 1. Map of the Cleveland Harbor area, showing the location of stations 1-9.

low of 5 to 100 or more. After this preliminary count of the more common plankters, the entire 1 ml. aliquot was examined at the same magnification, and the less abundant forms were enumerated. Where they were sufficiently abundant, the more common larger animal species were counted in a 10 ml. aliquot by the use of a dissecting microscope. Finally, the entire sample was scanned by use of a dissecting microscope and all of the less common larger animal forms were counted.

In those cases where centrifuged samples were used the procedure was similar: a 1 ml. aliquot was analysed carefully by use of the low power of a compound microscope fitted with a Whipple ocular micrometer and the remaining 9 ml. were scanned for larger animals by the use of the dissecting microscope.

Appropriate calculations were then made to estimate the number of phytoplankton cells per liter, and the volumes per liter of the more abundant phytoplankters. Numbers of the zooplankters were estimated per liter or per m^3 .

Seasonal distribution of the zooplankton

1. *Total zooplankton.* It was not deemed feasible in this study to determine the volumes of the various zooplankters for two reasons: irregularity of shape

of many of the species (especially Cladocera and Copepoda), and great variability of size among the individuals of many of the species. Lacking determinations of actual volumes, it was advisable to divide the zooplankters into two broad categories, namely those of smaller size (holozoic Protozoa, Rotifera and copepod nauplii), and those of larger size (adult and juvenile Cladocera and Copepoda). Figure 2 shows the seasonal distribution of these two categories of zooplankters, compared with the phytoplankters. Values for larger zooplankters are expressed in numbers per m.³, those for smaller zooplankters are expressed in numbers per liter, and those for phytoplankters are expressed in $\mu^3 \times 10^{-6}$ per liter. All values are averages of all the stations except station 1, which lay in the mouth of the Cuyahoga River, and gave results that were very different from those obtained at the other stations. Consideration of the horizontal distribution of plankters lies beyond the bounds of the present paper, and will be discussed elsewhere.

Unlike the phytoplankton, which with some exceptions exhibited a relatively uniform distribution from the surface to the bottom, the zooplankters (especially the Crustacea, but also to a lesser extent the rotifers) were regularly encountered in larger numbers in the deeper samples than in the shallower ones. All samples were taken in the daytime, and as is well known, many species of planktonic Copepoda, Cladocera and Rotifera migrate deeper into the water during periods of relatively intense light. In the discussion below the use of averages tends to even out the inequalities.

As shown in fig. 2, both the larger zooplankters and the smaller forms remained in relatively large numbers during the decline of the autumnal phytoplankton pulse in 1950. During the winter phytoplankton minimum the numbers of both zooplankton categories decreased almost to the disappearing point. The water was most barren of both categories of zooplankters in mid-February and in early March. The spring maximum of the smaller forms occurred in mid-March before the occurrence of the vernal phytoplankton pulse, whereas the spring maximum of the larger forms lagged somewhat behind the peak of the phytoplankton crop. Both groups of zooplankters were very abundant during the summer phytoplankton minimum, but both of them declined in numbers during the continuation of the period of impoverishment. The larger forms continued their gradual decline during the period of the autumnal phytoplankton maximum, while the smaller forms increased enormously in numbers, parallel to the increase of the volume of the phytoplankton. The numbers of smaller forms in September, 1951 were almost three times as great as those at the same date in the previous year, and they were more than twice as great as those obtained during the vernal maximum of 1951.

Elsewhere in Lake Erie, Chandler (1940) is the only author to report the seasonal distribution of total zooplankters. In western Lake Erie in 1938-1939 he found a maximum of about 105 zooplankters per liter in September of 1939, while the vernal maximum in 1939 (at the end of May) was about 130 per liter, and the fall maximum in 1939 was about 1,100 per liter (in September). He encountered a winter minimum (January, 1939) of 3 per liter, and a summer minimum of about 33 per liter. As in the Cleveland Harbor area, the vernal zooplankton maximum lagged behind the vernal phytoplankton pulse. On the other hand, the autumnal zooplankton maxima either preceded (1938) or occurred simultaneously with (1939) the autumnal phytoplankton maximum.

Chandler's results appear to indicate a lower zooplankton production in western Lake Erie at the time of his study than is shown for the Cleveland Harbor area in the present study. Translated to his units, the autumnal zooplankton maximum of 1950 for the Cleveland Harbor area amounted to 320 per liter, while that of 1951 was 1,792 per liter. The January minimum was 6 per liter (hence very close to Chandler's results), but the mid-summer minimum amounted to 186 per liter (early July), which is much higher than that found by Chandler.

Previous to the work of Chandler in western Lake Erie, Wright and Tidd (1933) had reported for the same region that the average number of the commonest Cladocera and Copepoda and of the copepod nauplii for the period between late May and early October was 37 per liter. This compares with an overall average of 14 specimens of the same categories per liter in the present study, during the same portion of the year. Thus Wright and Tidd found over 2.5 times as many of certain zooplankters as reported here. This is commensurate with the greater phytoplankton production of western Lake Erie, as discussed in the previous paper (Davis, 1954).

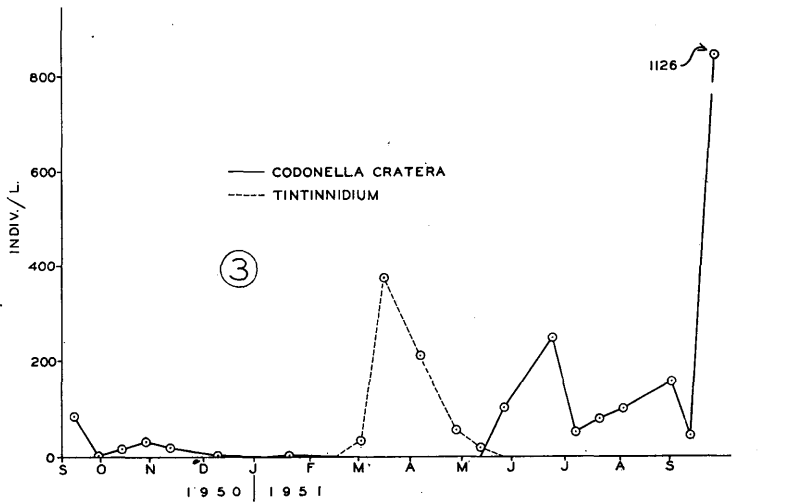
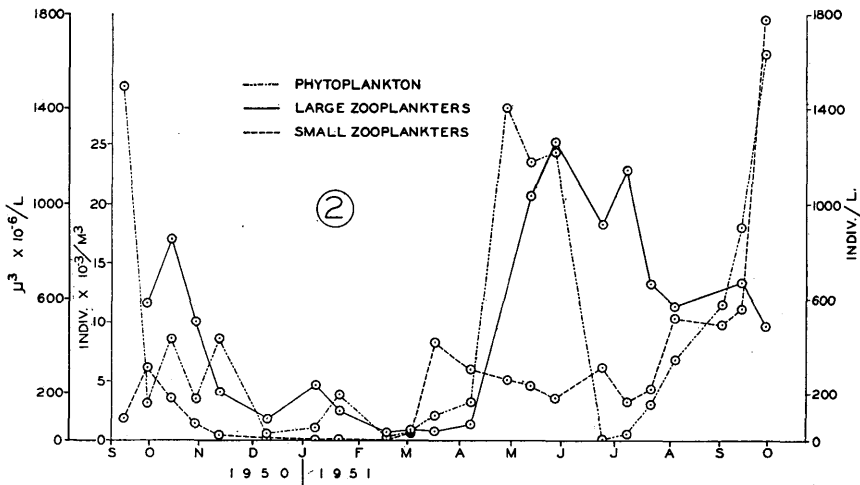


FIGURE 2. Seasonal distribution of smaller zooplankters (holozöic Protozoa, Rotifera and copepod nauplii) in numbers of individuals per liter, and of larger zooplankters (Cladocera and Copepoda) in numbers of individuals $\times 10^{-3}$ per m^3 , compared with the phytoplankton in $\mu^3 \times 10^{-6}$ per liter. Values given are averages of all the stations except station 1.

FIGURE 3. Seasonal distribution of *Codonella cratera* and of *Tintinnidium* sp. in number of individuals per liter. Values given are averages of all the stations except station 1.

Elsewhere in Lake Erie, and in the other Great Lakes, quantitative reports on zooplankton populations, or significant portions thereof, have not been presented, or they have been given in a form that is not comparable.

2. *Holozoic Protozoa*. As producers in the ecology of Lake Erie, the holophytic Protozoa were considered in the previous paper (Davis, 1954). Therefore in the present paper only those Protozoa that occupy a position as consumers of particulate organic matter will be considered. This group as a whole exhibited minimal abundance during December, January and February. During this period the average for all stations except station 1 was highest on January 20, but amounted only to 1.5 per liter on that date. Largest quantities were encountered in the spring and in the two autumnal periods, especially the autumn of 1951. The minimum that occurred in the late spring and in the summer was about 75 times as great as the mid-winter minimum.

A number of soft-bodied holozoic Protozoa were observed from time to time. Inasmuch as the preservative had distorted many of them beyond recognition, and none of them occurred in significant quantities at any time, they will not be reported here. *Arcella* and *Diffugia* shells occurred with considerable regularity, especially at station 1 in the River. They were not recorded because these forms are strictly tychopelagic, and furthermore, almost all the shells appeared to be empty shells from deceased organisms.

The tintinnids, *Codonella cratera* and *Tintinnidium* sp. were abundant at times. Their seasonal distribution is shown in fig. 3. The opacity of the tests made it impossible to ascertain in most cases whether the specimens were living or whether empty tests only had been captured. *Codonella cratera* fluctuated greatly from month to month, but only minimal numbers were encountered in December, 1950 and January, 1951, and none at all in February, March, April or the first part of May. In the autumn of 1950 numbers were rather low compared to the quantities estimated for the summer and fall of 1951. *Codonella* exhibited a mid-summer maximum with an average of 248 per liter at the time of the mid-summer phytoplankton minimum. Subsequently the numbers fluctuated, with limited, but not small crops, until on September 30 there was an enormous increase, with an average of 1,126 per liter, and with an absolute maximum of 3,506 per liter at the surface at station 8.

Vorce (1882), under the name *Tintinnus* sp., found this species ". . . during spring, summer and fall, quite abundant at times" in the Cleveland municipal water supply. Elsewhere in Lake Erie, Chandler (1940) reported it from June to September, 1939. The maximum was 66 per liter. It was not mentioned from the eastern basin of Lake Erie by Burkholder (1929a, b). In the other Great Lakes, it was listed as "frequent" in Lake St. Clair by Smith (1894), and the same term was employed by Kofoid (1896) to describe its occurrence in northern Lake Michigan (Traverse Bay area). More recently, Eddy (1927) reported up to 32 specimens per liter from Lake Michigan near Chicago in May, 1927. The same author (Eddy, 1934) said the species was "occasional" in Lake Michigan and in Lake Superior. It can be seen that, of the few quantitative estimates attempted in the Great Lakes, the present one is far greater than any other, especially in the fall of 1951, when the average for all stations except station 1 was about 17 times higher than that reported by Chandler (1940), and about 35 times as great as that reported from Lake Michigan.

Tintinnidium sp. appeared in large numbers only during March, April and the first part of May, 1951 (see fig. 3). The peak was attained in mid-March. An absolute maximum of 1,483 per liter was found at the surface at station 7 on March 17. After May 12 the species was not again encountered in the samples.

Chandler (1940), who is the only author who has carefully studied the year-round distribution of zooplankters in Lake Erie, listed no forms that might correspond with this species. Vorce (1882) encountered and figured a form with

at least a superficial similarity to the present species. He, however, considered it to be a shape variant of "*Tintinnus* sp.", other examples of which were clearly *Codonella cratera*.

Vorticella spp. were regularly encountered in the samples. Typically a benthic genus of Infusoria, some species are epizoid upon planktonic plants, such as *Anabaena*. Because it is not truly a planktonic genus, it was not enumerated in the samples obtained prior to April 6, 1951. Subsequent to that date the genus was counted because of its regular occurrence and relatively large numbers. As would be expected of epizoid forms, the numbers were roughly proportional to the amount of phytoplankton in the water. Largest numbers were found at the peak of the vernal pulse (an average of 134 per liter on April 28), and during the autumnal pulse (averages of 288 per liter on September 3; 229 per liter on September 14; and 152 per liter on September 30). Lowest numbers were found during the summer phytoplankton minimum, with an average of only 5 per liter on June 23.

In western Lake Erie, Chandler (1940) found the genus in most collections, "but not exceeding 15 per liter". In the eastern basin, Burkholder (1929a, b) reported it to be the most abundant protozoan in the plankton, with a maximum of 571 per liter in August, 1928. This maximum is similar to that obtained in the present study (600 per liter on September 3 at the surface at station 6).

3. *Rotifera*. As shown in fig. 4, the rotifers were most abundant in the two fall seasons and in late spring. Their fluctuations in numbers seemed to be more closely correlated with phytoplankton volumes than in the case of other major constituents of the zooplankton. Maximum quantities found during the entire study were on August 4, 1951, when there were 330 per liter, and at the end of September, 1951, when there were 490 per liter.

In the same general area of Lake Erie, Metcalf (1942) estimated the numbers of Rotifera at two stations off Lakewood in June, August and September of 1939. His method of collection precludes an accurate comparison of results. He reported rather large numbers in June, namely from 37 to 1,024 per liter, with the average of three collection dates at two stations being 398 per liter. His results for August and September are shown only graphically, but there was a maximum of about 37 during this period. Elsewhere in Lake Erie, Chandler (1940) found a seasonal distribution of total rotifers similar to that encountered in the present study. There was a maximum of 45 per liter in the autumn of 1938, a maximum of 75 per liter in May, 1939, and a maximum of 250 per liter in late September, 1939. Thus other quantitative estimates from Lake Erie are similar to those obtained in the Cleveland Harbor area in the present study.

Keratella cochlearis was the most common of the rotifers in the present study. Figure 4 shows the seasonal distribution of the species, numbers being averages per liter of all stations except station 1. The seasonal fluctuations of abundance are similar to those for all species of rotifers together. Highest average values were encountered at the end of September in each year. The absolute maximum was 956 per liter at the surface at station 7 on September 29, 1950.

A record was kept of the numbers of individuals bearing eggs, and these numbers are also depicted on fig. 4. At the end of September, 1950 and during October, from 3.4 to 12.1 percent of the individuals carried such eggs. Thereafter until May of the following year practically no reproducing specimens were seen, and the total number of individuals decreased greatly. During May the rate of reproduction increased to 21.2 percent. By the end of June, however, total numbers of this species were very small, and no evidence of reproduction was observed. Towards the end of July the total number of individuals had increased to 9 per liter, and the reproduction rate reached its peak for the year, namely 46 percent. This rapid reproductive rate resulted in a great increase of individuals, so that on the trip of August 4 there was an average of 247 individuals per liter. The reproductive rate and the total numbers then remained high in September.

Chandler (1940) found *K. cochlearis* to be among the most abundant of the rotifers of western Lake Erie, exhibiting a pulse in the fall of 1938 and another in the fall of 1939. There was a maximum of 150 per liter in September, 1939. Vorce (1881) said it was "common" in the Cleveland water supply. It was one of the two most abundant rotifers in Terwilliger's Pond (Ahlstrom, 1934), with important vernal and autumnal pulses. Ahlstrom estimated a maximum of 1,750 per liter in October. According to Kellicott (1896), it was "extremely abundant" in the water supply of Sandusky. In the eastern basin of Lake Erie, Burkholder (1929a, b) found the species to be "rather frequent" in July, but it was missing in September. He gave a maximum of 81 per liter in mid-August.

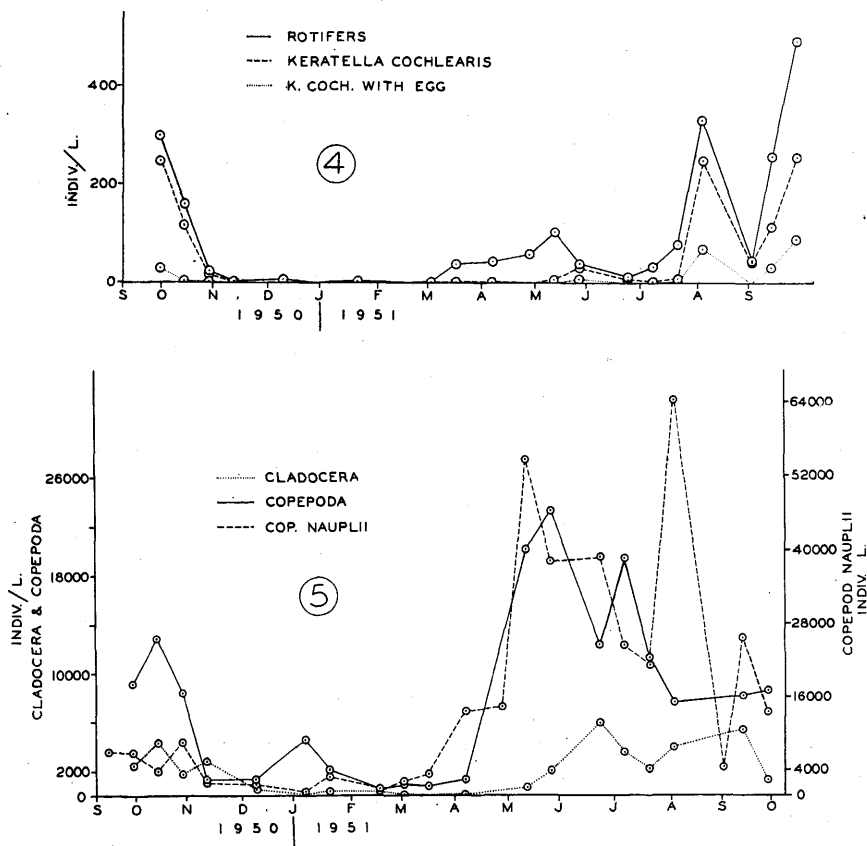


FIGURE 4. Distribution of total rotifers, of *Keratella cochlearis*, and of *K. cochlearis* with eggs in number of individuals per liter. Values given are averages of all the stations except station 1.

FIGURE 5. Distribution of Cladocera, of Copepoda, and of copepod nauplii in number of individuals per m.³. Values given are averages of all stations except station 1.

In the other Great Lakes, Jennings (1894) noted that it was "one of the most abundant" planktonic rotifers in Lake St. Clair. The same author (Jennings, 1896) found it more frequently than any other planktonic rotifer in northern Lake Michigan. Similarly, Ahlstrom (1936) recorded it to be "the most important species of rotifer numerically" in Lake Michigan. Previously Eddy (1927) had reported a maximum of 17 per liter of this species in Lake Michigan waters in the vicinity of Dunes Park. The species was listed by Eddy (1934) as "occasional" in Lake Michigan and "common" in Lake Superior.

In addition to *Keratella cochlearis*, the following rotifers were observed more or less commonly: *Asplanchna* sp., *Conochilus unicornis*, *Filinia longiseta*, *Keratella quadrata*, *Notholca longispina*, *N. striata*, *Polyarthra* spp., and *Synchaeta* spp. Table 1 sketches their seasonal distribution and gives a brief comparison with other records in the Great Lakes.

TABLE 1
Occurrence of Rotifera, other than Keratella cochlearis

Species	Period of occurrence (months)	Maximum abundance (numbers per liter in parentheses)	Other records, Great Lakes (numbers per liter in parentheses)
<i>Asplanchna</i> sp.	1950: S., D. 1951: S.	1950: S. 29.	Erie: Kellicott, '97 (very common) Chandler, '40 (4) St. Clair: Jennings, '94 (very abundant) Michigan: Jennings, '96 (very abundant)
<i>Conochilus unicornis</i>	1951: Jn., Jl.	1951: Jl. 7 (ave. 7; max. 36)	Erie: Burkholder, '29 (very common) Ahlstrom, '34 (45) Chandler, '40 (32) St. Clair: Jennings, '94 (very common) Michigan: Ahlstrom, '36 (very common)
<i>Filinia longiseta</i>	1951: My.	1951: My. 12.	Erie: Kellicott, '96 (not uncommon) Ahlstrom, '34 (900) Chandler, '40 (10) Michigan: Eddy, '27 (8)
<i>Keratella quadrata</i>	1951: Ap., My.	1951: My.	Erie: Chandler, '40 (6) Michigan: Eddy, '27 (8.5)
<i>Notholca longispina</i>	1950: N. 1951: Ma., My., Jn., Jl., S.	1951: My. 26 (ave. 5.5; max. 18)	Erie: Vorce, '81 (common) Kellicott, '97 (common) Chandler, '40 (18) St. Clair: Jennings, '94 (very abundant) Michigan: Jennings, '96 (regularly) Eddy, '34 (occasional) Ahlstrom, '36 (never commonly) Superior: Eddy, '34 (common)
<i>N. striata</i>	1951: My.	1951: My. 12 (ave. 7.5; max. 30)	Erie: Ahlstrom, '34 (55) Chandler, '40 (6) Michigan: Ahlstrom, '36 (sparingly)
<i>Polyarthra</i> spp.	1950: S., O. 1951: My., Jn., Jl., Au., S.	1950: O. 13 (ave. 31) 1951: My. 12 (ave. 9), S. 14 (ave. 87; max. 275), S. 30 (ave. 123)	Erie: Vorce, '82 (common) Kellicott, '96 (common) Burkholder, '29 (408) Ahlstrom, '34 (2,218) Chandler, '40 (50) St. Clair: Jennings, '94 (commonest) Michigan: Jennings, '96 (frequent) Eddy, '27 (16) Eddy, '34 (occasional) Superior: Eddy, '34 (occasional)
<i>Synchaeta</i> spp.	1951: Ma., Jl., Au., S.	1951: Jl. 21 (ave. 43; max. 84), S. 30 (ave. 9)	Erie: Kellicott, '97 (plentiful) Burkholder, '29 (small numbers) Ahlstrom, '34 (2,420) Chandler, '40 (70) St. Clair: Jennings, '94 (very abundant) Michigan: Ahlstrom, '36 (very common)

4. *Cladocera*. The seasonal distribution of the total Cladocera, including both juveniles and adults, is shown in figure 5. Few specimens were present in winter and in spring. During May the numbers increased, and on June 23 the maximum for the entire year was observed, amounting to an average of 5,870 per m.³ This maximum occurred at the time of the lowest point of the mid-summer phytoplankton minimum. The cladoceran population decreased, but not excessively, during the remainder of the summer. It increased again in August and September, but at the end of September, 1951 the population had decreased to a level somewhat below that observed at the same time in the previous year. During October and November (1950) the population fluctuated, but decreased steadily towards the winter low.

The production of Cladocera in the Cleveland Harbor area during the year September, 1950 through September, 1951, was apparently comparatively low. In the region of Greater Cleveland, in the summer of 1939, Metcalf (1942) estimated an average of 82,314 per m.³ at two stations on three dates in the latter half of June (max. 219,600 per m.³). During August and September he found a maximum of about 45,000 per m.³ As mentioned above, Metcalf's methods were only semiquantitative. In the western basin, Wright and Tidd (1933) calculated an average of 5,000 per m.³ for the entire period from late May to early October in 1929 and 1930. Chandler (1940) reported an average of 4,400 per m.³ for the period from September to mid-December, 1938, and an average of 5,000 per m.³ during the period from May 23 to September 25, 1939. In the eastern basin Wilson (1929a, b) showed the presence of large numbers of Cladocera, but his samples were not obtained quantitatively.

The distribution of the several species of Cladocera is shown in Table 2, along with a summary of the observations of other authors in the Great Lakes. The taxonomy of the genus *Daphnia* remains in an unsatisfactory state, as attested by various authorities, such as Wesenberg-Lund (1926), Brooks (1946) and Pennak (1953). No clarification can be brought to these matters here, and for the present purposes it is thought sufficient, following the example set by Chandler (1940), to distinguish three clearly defined forms, listed here as *Daphnia longispina*, *D. pulex* and *D. retrocurva*. Kiser (1950) would place the second and third forms as variants of a single species, and there is considerable indecision in the literature (Wesenberg-Lund, 1926; Berg, 1931, etc.), as to the propriety of separating *D. longispina* from *D. pulex*. The distribution of these three species of *Daphnia* in the Great Lakes is peculiar. *D. pulex* appears to be considerably less important in western Lake Erie than it is in the central and eastern basins. In Lake Ontario it has been listed as common, but the species has never been reported from any of the upper Great Lakes. Its abundance in Lake Winnipeg (Bajkov, 1930) indicates that its absence from the upper Great Lakes is not associated with latitudinal or geographic differences. The environmental factors preventing its occurrence need careful examination. The other two species occur more widely. An investigation of their quantitative distribution among the several Great Lakes would be of greatest interest.

5. *Copepoda*. The seasonal distribution of adult and juvenile copepodid stages of the Copepoda is shown on figure 5. The distribution of copepod nauplii is shown separately on the same figure. Largest numbers of the copepods occurred in the spring, lagging somewhat behind the development of the vernal phytoplankton pulse. The peak occurred on May 26, when the average was 23,240 per m.³. Relatively large numbers were also encountered during the period of the summer phytoplankton minimum, and during the fall months, and there was a small pulse during January.

Nauplii had a somewhat similar distribution, with, however, the greatest numbers in early August, 1951 (an average of 64,300 per m.³). During the vernal maximum the copepod nauplii began to increase greatly in numbers before the

TABLE 2
Occurrence of Cladocera

Species	Period when most common (months)	Maximum abundance (numbers per m ³ in parentheses)	Other Great Lakes records (max. number per m ³ in parentheses)
<i>Bosmina longirostris</i>	1950: S., O., N., D. 1951: My., J1., Au., S.	1950: S. 29 (ave. 100), O. 27 (ave. 200), N. 11 (max. 1,500). 1951: My. 12 (ave. 260), My. 26 (ave. 400; max. 1,600), Au. 4 (ave. 350; max. 1,200), S. 14 (ave. 600; max. 1,900).	Erie: Vorce, '81 (common) Wilson, '29 (common) Chandler, '40 (10,000) St. Clair: Birge, '94 (constant) Georgian Bay: Sars, '15 (not infrequent) Michigan: Eddy, '27 (most abundant)
<i>Ceriodaphnia reticulata</i>	1951: My.	1951: My. 26.	Erie: Chandler, '40 (small numbers)
<i>Chydorus sphaericus</i>	1951: My., J1., Au., S.	1951: Au 4.	Erie: Vorce, '82 (common) St. Clair: Birge, '94 (always present) Georgian Bay: Bigelow, '22 Michigan: Eddy, '34 (occasional) Superior: Forbes, '91 (frequent) Eddy, '34 (rare)
<i>Daphnia longispina</i>	1950: S., O. 1951: S.	1950: S. 29 (ave. 1,400; max. 13,600), O. 13 (ave. 2,500; max. 5,300). 1951: S. 14 (ave. 1,500; max. 7,200).	Erie: Bigelow, '22 (very abundant) Wilson, '29 (important) Chandler, '40 (most abundant—9,000) Ontario: Bigelow, '22 (very abundant) Georgian Bay: Bigelow, '22 (most abundant) Superior: Eddy, '34 (common)
<i>D. pulex</i>	1950: S., O. 1951: My., Jn., J1., Au., S.	1950: O. 13 (ave. 900) 1951: Jn. 23 (ave. 2,200; max. 12,300), J1. 7 (ave. 2,400; max. 5,700), Au. 4 (ave. 980), S. 14 (ave. 1,660; max. 5,300).	Erie: Wilson, '29 (most abundant) Chandler, '40 (3,000) Ontario: Bigelow, '22 (common)
<i>D. retrocurva</i>	1950: O. 1951: My., Jn., J1., Au., S.	1951: Jn. 23 (ave. 3,600; max. 10,700), J1. 21 (ave. 1,140; max. 5,500), Au. 4 (ave. 1,700; max. 4,300), S. 14 (ave. 850).	Erie: Bigelow, '22 (very abundant) Wilson, '29 (common) Chandler, '40 (4,000) Ontario: Bigelow, '22 St. Clair: Birge, '94 (frequent) Georgian Bay: Sars, '15 (rather common) Bigelow, '22 (abundant) Michigan: Eddy, '27 (300) Superior: Forbes, '91 (large numbers) Eddy, '34 (occasional)
<i>Diaphanosoma leuchtenbergianum</i>	1950: O. 1951: J1., Au., S.	1950: O. 13 (ave. 310). 1951: Au. 4 (ave. 600), S. 14 (ave. 650; max. 2,400), S. 30 (ave. 300).	Erie: Chandler, '40 (3,000) Georgian Bay: Bigelow, '22 Michigan: Eddy, '27 (common)
<i>Leptodora kindtii</i>	1950: S., O. 1951: J1., S.	1950: O. 27 (max. 400)	Erie: Bigelow, '22 (important) Chandler, '40 (1,000) Andrews, '48 St. Clair: Birge, '94 Georgian Bay: Sars, '15 (rather common) Bigelow, '22 Michigan: Forbes, '82 Eddy, '27, '34 Superior: Forbes, '91

increase of the adults and copepodids, even preceding slightly the inception of the vernal phytoplankton pulse. The vernal peak of nauplii occurred in mid-May, with an average of 54,600 per m.³

Metcalf (1942) studied the occurrence of copepods in the region of Greater Cleveland in 1939. His methods were only semi-quantitative, and were not fully comparable to the methods used in the present study. In 6 samples obtained at two stations in the latter half of June he estimated an average of 202,500 per m.³ (max. 951,500 per m.³). During August and September he showed a maximum of about 60,000 per m.³. In the western basin of Lake Erie, Wright and Tidd (1933) calculated an average for the entire period from late May to early October (1929 and 1930) of 16,000 copepods and 16,000 nauplii per m.³. In the present study the averages for the same portion of the year are 12,490 copepods and 22,600 nauplii per m.³. In the western basin Chandler (1940) found copepod pulses in autumn and spring in 1938 and 1939. In September, 1938 he reported a maximum of 40,000 per m.³. The spring pulse of 1939 extended from early April to mid-July, with a maximum of 70,000 per m.³ in late June. The summer minimum (in July) amounted to 20,000 per m.³, in contrast to the winter minimum of only 2,000 per m.³. The fall maximum of 1939 amounted to 40,000 per m.³. He described a similar seasonal distribution for copepod nauplii, with a maximum in late June of 40,000 per m.³. The results obtained by Wright and Tidd compare rather closely with the Cleveland Harbor area results, but Chandler found a larger quantity of copepods.

In the eastern basin of Lake Erie, Wilson (1929a, b) studied only non-quantitative samples. He found that copepods were less important in bulk than the Cladocera.

The seasonal distribution of the several species of copepods is shown in table 3, where previous records from the Great Lakes are also listed. No attempt was made to identify juvenile copepodid stages of the Cyclopoida, nor of *Diaptomus*. Attempts to separate the species of female *Diaptomus* in the counts were considered unreliable, and therefore only males are reported quantitatively as separate species.

TABLE 3
Occurrence of Copepoda

Species	Period when most common (months)	Maximum abundance (numbers per m ³ in parentheses)	Other Great Lakes records (max. number per m ³ in parentheses)
<i>Canthocamptus staphylinoides</i>	1951: My., S.	1951: My. 26 (max. 200)	Erie: Chandler, '40 (1,000) Michigan: Eddy, '27 (4,225) Superior: Forbes, '91
juvenile Cyclopoida	1950: S., O., D. 1951: My., Jn., Jl., Au., S.	1950: S. 29 (ave. 5,900; max. 20,400), O. 13 (Ave. 4,600), O. 27 (ave. 4,000). 1951: My. 12 (ave. 4,700), My. 26 (ave. 12,100; max. 23,600), Jl. 21 (ave. 7,000), S. 14 (ave. 4,000).	
<i>Cyclops americanus</i>	1951: Jl., S.	1951: S. 30.	Erie: Chandler, '40 (3,000) Andrews, '53 (17, 760)
<i>C. bicuspidatus</i>	1951: Ja., Mar., Ap., My., Jn.	1951: Ap. 6 (ave. 330), My. 12 (ave. 500; max. 1,800), My. 26 (ave. 500; max. 1,000).	Erie: Wilson, '29 (common) Chandler, '40 (7,000) Andrews, '53 (11,000) Great Lakes: Marsh, '95 (the common species) Georgian Bay: Sars, '15 (not infrequent) Michigan: Forbes, '82 (excessively abundant) Eddy, '27 (4,225) Superior: Forbes, '91 (the commonest) Eddy, '34 (common)

TABLE 3—(Continued)

Species	Period when most common (months)	Maximum abundance (numbers per m ³ in parentheses)	Other Great Lakes records (max. number per m ³ in parentheses)
<i>Mesocyclops leuckarti</i>	1950: S., O. 1951: My., Jn., Jl., Au., S.	1950: O. 13 (ave. 1,000; max. 1,900). 1951: Jl. 21 (ave. 520; max. 3,200), S. 30 (ave. 620; max. 2,700).	Erie: Chandler, '40 (8,000) Andrews, '53 (2,540) St. Clair: Marsh, '95 Georgian Bay: Sars, '15 (common) Michigan: Marsh, '95 Superior: Forbes, '91 (moderate numbers)
juvenile <i>Diaptomus</i>	1950: S., O. 1951: My., Jn., Jl., Au., S.	1950: O. 13 (ave. 6,000). 1951: My. 12 (ave. 12,300; max. 19,200), My. 26 (ave. 4,200), Jn. 23 (ave. 5,600), Jl. 7 (ave. 10,400; max. 19,600); S. 30 (ave. 3,900).	
<i>Diaptomus</i> spp. ♀	1950: S., O., D. 1951: Ja., Mar., Ap., My., Jn., Jl., Au.	1950: O. 27 (ave. 800). 1951: Ja. 5 (ave. 1,700), Jn. 23 (ave. 2,220; max. 4,200), Jl. 7 (ave. 3,300; max. 9,300).	
<i>D. ashlandi</i> ♂	1950: O. 1951: Ja., Mar., Ap., My., Jn., Jl., Au.	1951: Ja. 5 (ave. 900), Ja. 20 (ave. 700), Jn. 23 (ave. 1,000; max. 2,700), Jl. 7 (ave. 1,700; max. 10,000)	Erie: Wilson, '29 (numerous) Chandler, '40 St. Clair: Marsh, '95 (not abundant) Michigan: Marsh, '95 (common) Eddy, '27 (2,000) Superior: Marsh, '93 Eddy, '34
<i>D. minutus</i> ♂	1951: Mar., Ap., My., Jl.	1951: Ap. 6 (max. 700), My. 12 (ave. 150), Jl. 7 (ave. 120).	Erie: Chandler, '40 St. Clair: Marsh, '95 (most common) Georgian Bay: Sars, '15 Michigan: Eddy, '27 (1,600) Superior: Eddy, '34 (common)
<i>D. oregonensis</i> ♂	1950: S., O. 1951: Jl., Au.	1950: O. 27 (ave. 1,000; max. 2,800). 1951: Jl. 7 (ave. 150), Au. 4 (ave. 100).	Erie: Chandler, '40 Great Lakes: Marsh, '95 (not abundant) Georgian Bay: Sars, '15 (abundant)
<i>D. sicilis</i> ♂	(throughout the year)	1951: Ja. 5 (ave. 950; max. 1,700), Ap. 6 (ave. 200), Ap. 12 (ave. 300), Jl. 7 (ave. 300).	Erie: Wilson, '29 (abundant) Chandler, '40 Michigan: Forbes, '82 (immense numbers) Superior: Forbes, '91 (most abundant)
<i>D. siciloides</i> ♂	1951: Jl., Au., S.	1951: Jl. 7 (ave. 100; max. 800)	Erie: Chandler, '40
<i>Epischura lacustris</i>	1950: S., O. 1951: My., Jn., Jl., Au., S.	1951: My. 26 (ave. 600♂, 400♀, 4,200 juv.; max. 3,000♂, 1,900♀, 12,900 juv.).	Erie: Wilson, '29 (never very abundant) Chandler, '40 (8,000) St. Clair: Marsh, '95 (common) Michigan: Forbes, '82 (considerable numbers) Marsh, '95 (common) Superior: Forbes, '91 (common)
<i>Limnocalanus macrurus</i>	1951: Ja., Mar., My., S.	1951: Ja. 20 (max. 300), My. 12 (max. 700).	Erie: Chandler, '40 (1,000) Detroit River: Marsh, '95 Michigan: Forbes, '82 (abundant) Superior: Forbes, '91

DISCUSSION

In the previous paper (Davis, 1954), the sparsity of quantitative phytoplankton data for the Great Lakes was noted. The poverty of quantitative information on the zooplankton is even more striking. Only Chandler (1940) has seriously attempted to make a year-round quantitative study of all the zooplankters. Andrews (1953) made a careful study, but of three species only. Metcalf (1942) attempted a semi-quantitative study during a brief portion of the year in the Greater Cleveland area of Lake Erie. He contented himself with only three categories of zooplankters: Rotifera, Cladocera and Copepoda. Furthermore, his collections were made with an open net. Ahlstrom (1934) made a careful quantitative study of rotifers in Terwilliger's Pond, but not in Lake Erie proper. Elsewhere in the Great Lakes, only Eddy (1927)² has attempted a quantitative investigation. Eddy confined himself to a few quantitative collections at several different points in southern Lake Michigan during October, 1926 and May and July, 1927. In all other published studies, where the authors have gone beyond the simple approaches of taxonomy and distribution, only subjective estimations of abundance were made. Our lack of knowledge is the more regrettable, for it is commonly agreed that the North American Great Lakes constitute the largest and economically most important mass of strictly fresh water on the face of the earth.

The present results indicate a somewhat higher overall standing crop of zooplankton in the Cleveland Harbor area of 1950-1951 than that found by Chandler (1940) in the western basin in 1938-1939, but this apparently was the result of a relatively large number of the (volumetrically less important) smaller zooplankters in the present study. In an earlier year, Wright and Tidd (1933) had indicated larger zooplankton crops than comparable figures reported here. Their results were based upon only a limited portion of the zooplankton, namely the larger forms and copepod nauplii. Similar comparisons with other of the Great Lakes cannot be attempted.

In any study such as this it is the standing crop of the plankton that is determined, rather than the rate of plankton production, be it the phytoplankton or the zooplankton. Furthermore, when a series of stations at fixed locations is visited periodically, different water masses are being sampled on each visit. At times in the present study, totally different water masses were sampled at the outside stations, as compared with those closer inshore. For example, on January 20, 1951, at station 4, the volume of the total phytoplankton was between 6 and 7 times as great as that encountered at the other stations that were visited (Davis, 1954). On this date at the same station the average volume of *Melosira* sp. alone was $633 \times 10^6 \mu^3$ per liter, while the average of all the other stations together was $57.6 \times 10^6 \mu^3$ per liter. Thus at station 4 there was 11 times as much *Melosira* as the average at all the other stations. It is clear that at least two separate water masses were being sampled on that day. The nature of the investigation made it impossible to ascertain either the extent of such water masses or their movement and fate between collecting trips. More will be said below on this matter in connection with an attempt to interpret the sequence of plankton production.

An adequate interpretation of the seasonal changes of the plankton content of any body of water depends upon viewing the standing crop as the result of a dynamic series of events. The existing quantities (and the proportional quantities) of the plankton are the present status of its continuing development out of the standing crop of the past and into the standing crop of the future. Many

²Quantitative plankton analyses were reported by Tressler et al. (1953) for Irondequoit Bay, off Lake Ontario. Irondequoit Bay is nearly closed off from Lake Ontario, and there is no free circulation of water between the bay and the lake.

influences come to bear upon plankton production: physical factors such as temperature, density, diffusion currents, horizontal currents, turbulence, amount of solar radiation, turbidity, ice cover, etc.; chemical factors such as pH, quantity of plant nutrients, oxygen content, presence of trace elements, quantity of non-nutrient ions, the ratio of free CO_2 : HCO_3^- : $\text{CO}_3^{=}$, etc.; and biological factors such as quantity and nature of available organic food, quantity and nature of enemy organisms, interspecific and intraspecific cooperation and competition, metabolic rate, life span, rate of reproduction, etc. As pointed out by Wautier (1949) in his excellent discussion of these ecological principles:

"Si l'on tente de préciser les raisons de la complexité du milieu physique, on constate qu'elles sont multiples. Chaque facteur n'agit pas isolément, mais en liaison avec les autres. Les actions ne s'ajoutent pas mais se combinent, chaque facteur agissant sur tous les autres et étant, à l'inverse, affecté par chacun d'eux. Les différents facteurs n'interviennent d'ailleurs pas tous de manière forcément simultanée; certains peuvent avoir agi antérieurement à d'autres, favorisant, modifiant ou contrecarrant leurs effets. Il y a plus: l'action de certains facteurs modifie plus ou moins la sensibilité des organismes à d'autres facteurs."

The response of a species to one factor often varies as other factors change. In the previous paper (Davis, 1954), for example, the diatom *Asterionella* sp. was shown to be present in the plankton throughout the year. During most of the time it was subordinate to other diatoms in quantity, but during much of the winter and early spring season it was the dominant phytoplankton. This condition has also been observed in the western basin of Lake Erie (Chandler, 1940, 1942, 1944; Chandler and Weeks, 1945). One might infer from all this that *Asterionella* production was favored by the cold water conditions of winter and early spring. On the other hand, during the period of the spring phytoplankton maximum in the Cleveland Harbor area, when temperatures were rising rapidly, *Asterionella* remained present in approximately the same numbers (with a slight decrease) as before the vernal pulse (see Davis, 1954, fig. 15). It is conceivable that the temperature conditions of late spring were even more favorable for this species than the cold of winter, but that other factors, such as the antagonistic effects of other phytoplankters, or competition for plant nutrients in the period of enormous phytoplankton production, retarded its production.

Asterionella was practically absent during the summer months, but this could not have been the result of the deleterious effects of high water temperatures, as indicated by the fact that with the reduction of the zooplankton at the beginning of August, *Asterionella* produced its biggest standing crop of the year (though it was subordinate to other forms). At the beginning of August the water temperature stood at its seasonal peak. The estival sparsity of *Asterionella* must have been caused by other factors, such as the high grazing rate of the myriads of zooplankters present at that time.

Similarly, the copepod, *Diaptomus ashlandi* occurred in largest quantities in mid-winter and in mid-summer, though it was present at all times of the year. The large number in mid-summer undoubtedly was associated with the great production of phytoplankton during the warm months, but the potential numbers probably were not attained because of stiff competition from other larger zooplankters (especially *Daphnia*). During the winter there was little competition from other zooplankters, and *D. ashlandi* was thus able to take advantage of a relatively small phytoplankton pulse at that time. The lack of a pulse of adult *D. ashlandi* during the periods of the spring and of the fall phytoplankton maxima may have been associated with breeding activities, which were not determined in this study. The spring phytoplankton maximum was preceded by $2\frac{1}{2}$ months of low phytoplankton production, which would be detrimental to the development of nauplii and other juveniles of *D. ashlandi*. Furthermore, active breeding in the near-freezing temperatures of January does not appear probable (few females of *Diaptomus* with egg cases were observed at that time). If the females were

as abundant as the males in mid-summer (this was the case for females of all species of *Diaptomus* together, and *D. ashlandi* males were the most abundant of all species of the genus), and if they bred commensurate with their numbers, then it is possible that their numerous offspring succumbed in large numbers a) to a relative lack of food during late July, and b) to a large increase of planktonic and other predators as a result of the enormously rich food supply of mid-summer. The increase of predators is suggested by the fact that the predator *Leptodora kindtii* was most common during September.

Such explanations as those above are necessarily hypothetical in the present state of our knowledge, but the hypotheses can be tested by more adequate field studies, and it is planned to make such studies in the future.

The striking nature of the seasonal fluctuations of the phytoplankton and the zooplankton has led inevitably to a number of attempts to unravel the intricacies of cause and effect that are involved. Some of the early workers (e.g., Apstein, 1896), as well as some more recent, have observed the small quantities of plankton during the cold months of the year, and the large masses of blue-green and green algae often occurring in the warmest months, and have concluded that the controlling factor for phytoplankton production, and hence indirectly for zooplankton production, is the temperature of the water. On the basis of other evidence, however, other early authors concluded that it is not the temperature, but solar radiation that is the controlling factor. This is the stand taken, for example, by Zacharias (1907). Still other authorities have adopted a somewhat more dynamic point of view, namely that the basic causative factor is neither the temperature nor the radiant energy directly, but changes in the plant nutrient content of the water. According to this third conception, the spring and fall overturns refresh the nutrients by a mixture of the nutrient-rich deeper layers of water with the nutrient-poor upper layers, hence allowing the vernal and autumnal phytoplankton pulses to occur. The rapid growth of the phytoplankton depletes the nutrient salts and results in the summer or winter phytoplankton minimum. Different quantities and proportions of the important minerals (nitrates, phosphates, silicates, etc.), favor different groups of phytoplankters (diatoms, greens, blue-greens, etc.). Among the foremost proponents of the plant nutrient hypothesis are Pearsall (1932), and Rodhe (1948).

The voluminous accumulation of data from the study of many sorts of lakes and ponds in many countries has forced most recent authors to abandon the attempt to explain seasonal fluctuations on the basis of any one controlling factor. This data includes, for example, the work of Chandler (1940), who showed that the entire vernal phytoplankton pulse of 1939 in western Lake Erie occurred beneath the ice cover, and hence at winter temperatures. In the present study there was a marked mid-January phytoplankton and zooplankton pulse, when water temperatures were only a fraction of a degree above freezing, and when solar radiation was at a minimum. Many lakes, including western Lake Erie, and at least that portion of the central basin reported here, almost never exhibit temperature stratification, and hence there are no vernal and autumnal overturns. Frequently such lakes have marked vernal and autumnal phytoplankton pulses. Furthermore, many temperate zone lakes do not have regular spring and fall maxima, as shown by Pennak (1946, 1949) in certain Colorado reservoirs.

The "stubborn facts" have forced authors in recent years to adopt generalizations that reflect the interaction of more than one factor. Findenegg (1947) and Steleanu (1953) stressed the interaction of both temperature and light. According to Findenegg, the winter plankton population consists of cold-water, weak-light species, the spring population of cold-water, strong-light species, the summer plankton of warm-water, strong-light species, and the fall plankton of warm-water, weak-light species. In the present study, both the vernal and autumnal phytoplankton maxima were dominated by *Melosira* sp. (Davis,

1954), and as mentioned above, *Asterionella* sp. dominated the winter phytoplankton, but there was a much larger biomass of this form at the peak water temperatures in the early fall. According to Findenegg's scheme, *Melosira* must therefore be both a cold-water, strong-light form and a warm-water, weak-light form, and *Asterionella* must be placed in the cold-water, weak-light category, or in the warm-water, strong-light category, depending upon the season.

Innate internal rhythms of reproduction, nutrient supply, and seasonal flooding have been suggested as causative agents by Carpenter (1928), who concluded that some local factors probably always contribute to the complex influences affecting plankton production. Needham and Lloyd (1937) correlated temperature, spring and fall overturns and grazing by zooplankters as influences in seasonal phytoplankton fluctuations. The interaction of the rate of multiplication and the rate of depletion was discussed by Ruttner (1952) and Ruttner, Frey and Fry (1953). These authorities suggested that the rate of multiplication is determined largely by the combination of the two factors of Findenegg—solar radiation and temperature—, but they added that plant nutrients are important. The rate of depletion is influenced primarily by sinking and sedimentation, modified by the water inflow and outflow, and through consumption by grazers and predators.

Recently McCombie (1952) has reviewed the literature concerning the influence of physical, chemical and biochemical factors on phytoplankton quantity. Although the body of his paper clearly indicates the complexity of the interactions of the several factors, he follows the tendency towards oversimplification that dominates much biological thought today by concluding: “. . . this cycle is caused chiefly by the seasonal change in water temperature resulting from the change in solar radiation.”

After summarizing many of the theories concerning the causes of seasonal fluctuations of the plankton, Welch (1952) drew the only feasible conclusion: that it is probably impossible to use any single factor or influence to explain the periodic maxima and minima, but that the fluctuations are the result of the interplay of influences acting in combination and at different intensities. Such conclusions, however, remain vague generalizations unless the principles are illustrated by concrete applications to actual seasonal cycles. Even Wautier (1949), whose clarity on these matters is unsurpassed, inadvertently discouraged further research into these matters when he figuratively threw up his hands in dismay and stated:

“Un telle complexité du milieu physique rend très difficiles, dans l'état actuel de la science, l'analyse rationnelle et la compréhension, même partielles, des relations entre le milieu et les organismes.”

Certainly our knowledge has advanced to the stage where we may profitably attempt to analyze the interplay of influences determining the seasonal fluctuations of plankton abundance.

In the following such an analysis will be attempted to explain the general progress of events during the year in the Cleveland Harbor area. Each of the hypotheses that is suggested can easily be tested through a planned program of further field observations and laboratory culture experiments. At this time explanations of the fluctuations of abundance of individual species will not be attempted, but only the fluctuations of large groups. Figure 2 of the present paper shows graphically most of the events under consideration. Other figures should also be consulted.

In the fall of 1950 there was a large standing crop of phytoplankton, and of zooplankton as well, though the latter apparently had not at first reached its autumnal maximum. During October and early November the water temperatures fell rapidly (Davis, 1953; Davis and Roney, 1953), and solar radiation

decreased sharply. This inevitably resulted in a reduction of the rate of metabolism and of reproduction among the phytoplankters. At the same time there was a considerable increase of the zooplankton, perhaps because of a reduction of the number of predators. As a result primarily of these three factors, the phytoplankton declined in importance, so that by early December the winter phytoplankton minimum had firmly set in. Quantities of the zooplankton, especially the larger forms, declined more slowly (along with the decrease of their food supply), but by early December these also had declined to their first winter minimum.

During January, both the phytoplankton and the larger zooplankton forms increased to a mid-winter maximum, but peculiarly, the zooplankton maximum preceded the phytoplankton maximum. This may have been caused by the sampling of different water masses in early January as compared to late January—water masses concerning whose history we have no evidence—or it may indicate that phytoplankton productivity in early January was higher than that indicated by the measurements of the phytoplankton standing crop. In the latter case the zooplankters would keep the phytoplankton crop grazed down, but with the disappearance of the bulk of the zooplankters (through old age, predators, starvation, etc.), the phytoplankton would increase to its mid-winter pulse. More detailed study of mid-winter productivity is needed to clarify this problem.

In March the increase of solar radiation, probably with other factors, appears to have increased the productivity of the phytoplankton considerably. This was indicated, not by any great increase of the standing crop of the phytoplankton, though there was a slight increase. Rather, it was indicated by a considerable increase in the quantity of the smaller zooplankters. This increase preceded by 6 weeks the vernal phytoplankton maximum. On the other hand, because of the slower breeding rate of the larger zooplankters, their vernal maximum lagged behind the vernal phytoplankton maximum by two weeks. It is interesting to note in this connection that copepod nauplii and cladoceran embryos (in their parental brood pouches) increased strikingly in abundance *before* the vernal phytoplankton pulse, but adults of these two groups, and copepodid stages of the Copepoda, did not increase greatly until after. Possibly the slight decline of the smaller zooplankters during the period just before and during the vernal phytoplankton maximum was the result of competition with the growing population of nauplii, and later of older stages of Copepoda and Cladocera.

As described in the previous paper (Davis, 1954) the decline of the vernal phytoplankton maximum was very sudden and precipitous. It would seem improbable that such a sudden and complete change could take place in such a short period in a single water mass. Therefore it is postulated that around the first of June a new water mass, barren of phytoplankters, encroached upon the Cleveland Harbor area from farther west in the lake. Presumably the same general changes would have taken place in the previous water mass, however, given sufficient time.

With the disappearance of the vernal phytoplankton maximum the mid-summer maximum of larger zooplankters appeared, associated with the rich food supply of the previous period. It seems apparent that there was no decrease of phytoplankton productivity, despite the sparsity of the standing crop, contrary to the stated or implied assumptions of most previous authors (e.g., Welch, 1952). It would seem that the large quantity of actively feeding zooplankters kept the standing crop decimated by incessant grazing, and in reality phytoplankton productivity remained as high, or nearly so, as before. The effect of grazing in the development of the mid-summer phytoplankton minimum has been suggested previously by Needham and Lloyd (1937).

During the summer and ensuing fall the numbers of the larger zooplankters steadily decreased, possibly in connection with competition for the existing food,

and with the increase in the number of predators such as *Leptodora kindtii*. Ultimately this decline reached a point where phytoplankton production again exceeded phytoplankton destruction, and the autumnal phytoplankton maximum set in. The increase in available food, and the reduced competition of large zooplankters then allowed the smaller zooplankters, with their short life histories, to increase enormously.

In all the above, an important direct grazing effect of the zooplankters is assumed, following the example of Riley, Stommel and Bumpus (1949). Some recent authors have cast doubt upon such a direct effect of grazing (see Pennak, 1946), but important experimental and observational work, some of it very recent (e.g., Pennington, 1941 and Bainbridge, 1953), supports the contention that the zooplankters graze directly upon both the larger phytoplankters and the nanoplankters, and thus directly affect the size of the standing crop of the phytoplankton. The results of the present study cannot adequately be explained other than on the basis of a direct grazing effect.

The above analysis leaves many questions unanswered, especially questions about the fluctuations of individual species, but also such questions as the great difference between the fall season of 1950 and that of 1951 as regards the production of smaller zooplankters (fig. 2). It also is undoubtedly true that many important influences have been omitted from the discussion. For example, Lefèvre, Jakob and Nisbet (1952) have proven the importance of self-produced antibiotics in the growth of plankton algae, as has Rice (1954). Factors such as this may have had an influence in the decline of phytoplankton pulses. Many authors have emphasized the necessity of plant nutrients (see above). It is possible that increased nutrients entering the lake with the spring run-off influenced the development of the vernal phytoplankton maximum, and that decreased nutrients influenced the development of the estival minimum. These matters need to be examined further for clarification. In this connection, Juday *et al.* (1928) have shown in certain Wisconsin lakes that as much phosphorus was present in the summer as during the spring phytoplankton maximum, and that there was no increase of the phosphorus content of the water just preceding the vernal phytoplankton pulse. In the present results, there was a marked mid-winter phytoplankton pulse (Davis, 1954, and fig. 2 above), supporting the contention that low nutrient content was not the primary cause of the winter minimum. A continuing zooplankton maximum during the summer phytoplankton minimum is clear evidence of continuing phytoplankton production, and hence of adequate quantities of plant nutrients. An additional influence—that of turbidity—is sometimes important in limiting plankton production. In the present study, turbidities were measured (Davis, 1953; Davis and Roney, 1953), but there was no apparent correlation with plankton crops.

It is planned to follow up as many of these problems as time permits.

SUMMARY

1. The results of the analysis of quantitative zooplankton samples taken on 23 trips at nine stations in the Cleveland Harbor area of Lake Erie are given. The trips were undertaken in the year September, 1950 through September, 1951. Previously there has been only a single year-round quantitative study of the zooplankton in the Great Lakes. This was the study by Chandler (1940) in the western basin of Lake Erie.

2. The larger zooplankters (Cladocera and Copepoda) occurred in largest numbers during the summer period, when the phytoplankton was at its summer minimum. There were, however, large numbers also in both autumn seasons, and there was a small pulse (mostly Copepoda) in mid-winter. The quantity of these larger zooplankters appears to be smaller than that reported from the western basin.

3. The maximum of larger zooplankters in the fall of 1950 and that setting in during the late spring of 1951 lagged behind the occurrence of the phytoplankton maxima.

4. The smaller zooplankters (holozoic Protozoa, Rotifera, and copepod nauplii) were most abundant in the spring of 1951, and in both fall seasons. The spring maximum was larger than the maximum of September, 1950, but the fall maximum in 1951 (late September) was many times greater than either of the other two. The quantity of the smaller zooplankters in the Cleveland Harbor area considerably exceeded the quantities reported from the western basin.

5. The maxima of the smaller zooplankters tended to accompany the occurrence of the maxima of phytoplankton, or they even preceded the diatom maxima. Thus, the vernal maximum of 1951 occurred in late March, 6 weeks before the vernal phytoplankton maximum.

6. The seasonal distribution of the various species of holozoic Protozoa, Rotifera, Cladocera and Copepoda are tabulated, and compared with the results of other observers elsewhere in the Great Lakes. In general, the larger species occurred in smaller quantities than in the western basin of Lake Erie, while some of the smaller species occurred in larger quantities.

7. The effects of the diurnal vertical migration of the planktonic Crustacea was evident in the unequal distribution of these forms between the surface samples and the samples collected at 6.5 m. All samples were collected in the daytime, and the deeper samples averaged much larger numbers of these forms.

8. The necessity of distinguishing standing crops of plankton from plankton productivity is emphasized. Also, in such studies as the present one, it is pointed out that different water masses are sampled on every collected trip, and sometimes even on one collecting trip at different stations. Examples are given from the results.

9. An attempt is made to analyze the course of events in plankton production during the year. The complexity and interplay of the influences is stressed. The seasonal history of the diatom genus *Asterionella* and of the copepod *Diaptomus ashlandi* are used as examples of the manner in which the influence of one environmental factor varies as other environmental factors are altered. The decline of the autumnal phytoplankton maximum is thought to be the result of lower reproductive rates and a great amount of grazing by zooplankters. A great increase of phytoplankton production was indicated in March by a considerable increase in smaller zooplankters, 6 weeks before the onset of the vernal phytoplankton pulse. The decline of the vernal phytoplankton maximum is thought to have been caused primarily by the heavy grazing activity of the numerous zooplankters during the summer months. The onset of the autumnal phytoplankton maximum is thought to have been caused by a reduction of the larger zooplankters, which in turn was caused by a combination of a reduction of the food supply and an increase in the numbers of predators.

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